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Research Article

Difference in sale strategies drive spatial heterogeneity in collection pressure through online auctions: the role of body colour variation in the Japanese freshwater crabs, *Geothelphusa dehaani* species complex

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Abstract

The increase in online sales of living organisms has raised considerable concerns about its impact on wildlife. High demand for specific biological traits can intensify collection pressure via wildlife trades, yet the effects of colour variations and their geographical distribution on regional collection pressure remain poorly understood. This study analysed 11 years of transaction data — including, number, volume, price, date, colour types (DB: dark brown; RD: red; SB: sky blue; OT: other colours; and Mix) and collection locality — for the *Geothelphusa dehaani* species complex, renowned for its regional colour variations and aquarium popularity. Contrary to expectations that rarer colouration types (SB and OT types) are collected in higher numbers, the wild *G. dehaani* species complex collection pressure via online auctions (i.e. selling volume of wild-caught individuals) was higher for the common DB type (15,493 individuals) than for the rarer SB and OT types (2,073 and 173 individuals, respectively). This difference arose from a mechanism based on two distinct strategies linked to the colour traits and geographical distribution: the DB type followed a low-profit, high-sales (LPHS) strategy, selling large quantities at low unit prices, while the SB and OT types employed a high-profit, low-sales (HPLS) strategy, selling fewer individuals at higher unit prices. These findings highlight how colour variations influence online auction sales strategies and may negatively impact wildlife populations due to heterogeneous collection pressure at regional or local levels. Given the potential for rapid shifts of such mechanism driven by the appearance of mass sellers or the taxonomic revisions (i.e. additional value by a new species), our study suggests that implementing nuanced regulatory measures — for example, annual limits on the number of living animal auctions per taxon per year — could mitigate the risks associated with the diverse collection pressures through online auctions.

Key words: Aquarium trade, auction strategy, biodiversity, conservation, consumer preference, market demand

Introduction

Online wildlife trade poses a significant threat to biodiversity conservation (Hughes 2021; Soriano-Redondo et al. 2023). The internet's rapid growth has broadened opportunities for living animal commerce (Kikillus et al. 2012; Mazza

et al. 2015; Olden et al. 2021), enabling peer-to-peer transactions amongst non-professionals (Olden et al. 2021; Takaku and Morosawa 2021; Ueno and Eguchi 2023). This shift has led to a decline in ethical standards and an increase in challenges, including illegal trade, wildlife population exploitation and the introduction of non-native species (e.g. Nijman (2010); Natusch and Lyons (2012); Mazza et al. (2015); Vaglica et al. (2017); Takaku and Morosawa (2021); Soriano-Redondo et al. (2023)). In particular, the growing availability of wildlife online raises concerns about intensified collection pressure on these species and populations (Soriano-Redondo et al. 2023).

Identifying factors that influence the value and volume of online wildlife trade and assessing their effects on species or populations, are key challenges for biodiversity conservation (Tournant et al. 2012; Williams et al. 2018). Unique colour morphs often command higher prices (van Wilgen et al. 2009; Pienaar and Sturgeon 2024), with interspecific differences, colour polymorphisms and anomalies (e.g. albinism) across various taxa. Rarer colour morphs associated with specific geographical distributions (i.e. non-random distributions) may be selectively harvested, exacerbating the risk of local extinction through anthropogenic Alee effects (AAEs), where the rarity increases due to collection (Courchamp et al. 2006; Hall et al. 2008; Holden and McDonald-Madden 2018). This issue spans multiple taxa, including mammals, birds, reptiles, amphibians, fish and insects (Courchamp et al. 2006; Holden and McDonald-Madden 2018). However, previous research has primarily focused on rare species (e.g. Sajeva et al. (2013); Vaglica et al. (2017); Holden and McDonald-Madden (2018); Sánchez-Mercado et al. (2020)), neglecting the nuances of collection pressure and sales related to colour traits on a common species (Lyons and Natusch 2013; Militz et al. 2018). In particular, increased collection pressure is likely to elevate negative impacts more dramatically at the population level than at the species level. For instance, populations of the green python *Morelia viridis*, known for its rare colouration and high collector demand, have suffered from overexploitation (Lyons and Natusch 2013). Therefore, examining the effects of colour traits not only at the interspecific level, but also at the intraspecific level, is crucial for gathering information to mitigate exploitation of wildlife through online trade.

Wildlife trade is shaped not only by consumer preferences, but also by economic market dynamics (McNamara et al. 2016). Analysing online auction data provides insights into consumer demands and supply responses (Hinsley et al. 2015; Olden et al. 2021). Auction descriptions often include details about origin, characteristics, rarity and individual counts, which influence the pricing and bidding patterns, reflecting demand magnitude. Consequently, such analyses reveal the conditions of the living wildlife trade, incorporating both biological attributes and market dynamics, such as price and transaction volume. For example, Takaku and Morosawa (2021) categorised sales of endangered Japanese freshwater fish into three patterns, based on transaction data from the domestic auction platform, Yahoo! auction: the main channel type (high transaction volume and value), the low-margin high-volume type (numerous transactions, but lower unit prices) and the high added value type (high unit prices despite fewer transactions). This study not only describes these categories, but also suggests that transaction volume variation may lead to different levels of collection pressure via online auctions across species or populations.

This methodology aids in classifying consumer preferences and predicting the outcomes of intervention strategies aimed at resulting local extinction risks.

Freshwater crabs serve as an illustrative case study for understanding variations in wildlife trade, including online auction sales. True freshwater crabs have adapted to freshwater, semi-terrestrial or terrestrial environments and can complete their life cycle independently of the marine ecosystem (Yeo et al. 2008; Shy et al. 2020). Over 1,400 freshwater crab species have been identified globally (Cumberlidge 2016), many of which are colourful and appealing to aquarium hobbyists (Yeo et al. 2008). In Japan, *Geothelphusa dehaani* sensu lato (Japanese name: "Sawagani") has historically been used for food items and medicines (Chokki 1993; Shy et al. 2020) and is popular as a pet, due to its accessibility and ease of care. This group had been considered to be a single species, *G. dehaani*, having wide distribution across the Japanese archipelago, including Hokkaido, Honshu, Shikoku, Kyushu and surrounding islands, as well as parts of South Korea (Toyota and Seki 2019; Lee et al. 2019; Sugime et al. 2022; Takenaka et al. 2023). Recent phylogeographic studies implied the presence of the cryptic species or deeply divergence populations within *G. dehaani* sensu lato (Takenaka et al. 2023; Kunishima and Takata et al. 2025). In addition, a recent morphological study has updated the taxonomic status of *G. dehaani* sensu lato (Naruse and Ng 2024), so that they now include *G. dehaani* sensu strico, *G. amakusa* and *G. mutsu*. These findings suggest a potential future taxonomic revision for the *Geothelphusa dehaani* species complex, highlighting the needs to assess wildlife trade demands and develop conservation strategy as the *G. dehaani* sensu lato may include several species.

Geothelphusa dehaani species complex exhibits body colour variation, traditionally classified into three main types: DA (dark), RE (red) and BL (blue) (Suppl. material 1; Chokki 1976, 1980). Each type exhibits distinct non-random geographical distributions in Japan, with DA being most widespread and RE and BL being more localised in specific areas (Kunishima and Takata et al. 2025). In addition, rare colour individuals, likely individual variations have been occasionally found (e.g. yellow, purple and pink; Furuya and Yamaoka (2017); Kunishima and Takata, unpublished data). Given uniquely coloured individuals typically command higher prices, specific colour individuals or populations with limited distribution, such as BL, as well as rare colour individuals, may face greater collection pressure via wildlife trades than the more abundant DA. Although these colour types do not entirely correspond to nuclear SNP genetic structures (Kunishima and Takata et al. 2025), high market demand for specific colour types may lead to anthropogenic negative impacts, such as the decline of population density and genetic diversity, through wildlife trades.

This study aims to determine how colour variation influences online auction sale strategies for the *G. dehaani* species complex and, consequently, how differences in colour-based sale strategies, along with non-random geographical distribution of colour variation in the *G. dehaani* species complex, may negatively impact specific wild populations through online auctions. To achieve this goal, the author examined the differences in transaction trends of distinct body colouration traits, analysing prices, volumes and individual counts of the *G. dehaani* sensu lato from completed transactions on Yahoo! Auction, Japan's leading online auction platform, in a period of 11 years. This study also evaluated the collection pressure through online auctions, based on basic transaction

volumes and collection locations of the wild *G. dehaani* species complex. I predicted that high volume auction-sales of SB and OT types, combined with their limited and non-random geographical distributions, would lead to spatial heterogeneity in high collection pressure through online auctions. Findings of this study indicate the potential negative impact of private living animal sales on colour polymorphic wildlife, particularly within the context of the expanding online auction market for living animals.

Materials and methods

Data collection and screening

This study utilised an 11-year dataset of successful *G. dehaani* sensu lato transactions from January 2013 to December 2023. Auction data were retrieved using the keyword in katakana "Sawagani," which translates to freshwater crabs in Japanese, from AucFan, a comprehensive online auction database (download date: 23 January 2024). AucFan enables users to search and compare product and price information across various e-commerce auction sites, including Yahoo! Auction, the primary platform for trading live animals in Japan (AucFan.com 2024). AucFan's historical transaction records facilitate comparisons across years. All transactions used in this study were within country.

The collected auction data included 3,988 transactions involving 17 species (*G. dehaani* sensu lato, *G. albogilva*, *G. exigua*, *G. grandiovata*, *G. koshikiensis*, *G. kumejima*, *G. mariginata*, *G. minei*, *G. sakamotoanus*, *G. tenuimanus*, *Candidiopotamon kumejimense*, *C. okinawense*, *C. tokashikiense*, *Mediapotamon* sp., *Candidiopotamon* sp., *Ryukyum yaeyamense* and unverifiable freshwater crab species), as the name "Sawagani" is used not only for "*G. dehaani*", but also as a root in the standard Japanese names of other freshwater crab species in the genus *Geothelphusa* and those in related genera (e.g. Yakushima-sawagani for *G. marmorata* and "Okinawa-minami-sawagani" for *Candidiopotamon okinawense*). As species from foreign countries or the Ryukyu Islands possess added value beyond colour traits (Kunishima, unpublished data), this study focused exclusively on the *Geothelphusa dehaani* sensu lato, narrowing the analysis to 3,431 online auction transactions. As noted in the Introduction section, *G. dehaani* sensu lato now includes cryptic species or deeply divergent populations (Takenaka et al. 2023; Kunishima and Takata et al. 2025). Recently, Naruse and Ng (2024) designated the lectotype of *G. dehaani* sensu stricto and described two new Japanese species — *G. amakusa* (from Kamishima Island, Amakusa Island, Kumamoto Prefecture) and *G. mutsu* (from Takizawa, Aomori Prefecture). However, their precise distributions remain uncertain and, at the time of online auctions during survey periods, *G. dehaani* sensu lato ("Sawagani") was recognised as a single species. It is likely that transactions did not include *G. amakusa* and *G. mutsu* during survey periods, considering their body colouration with body size and collection location (Naruse and Ng (2024); i.e. sky-blue carapace in large individuals or orangish carapace in small individuals and Kumamoto Prefecture for *G. amakusa*; dark brown carapace and Aomori Prefecture for *G. mutsu*). However, all freshwater crabs traded as "Sawagani" during this survey period are treated as the *G. dehaani* species complex in this study.

The dataset was enhanced by adding information from each transaction's page to the initial data retrieved from the AucFan site. The refined dataset for the *G. dehaani* species complex included several variables: title, traded category, collection location (Prefecture), colouration type, origin, number of individuals, opening-price, closing-price, difference between opening-price and closing-price (price-difference), price per individual, traded date, seller ID, seller category and shipping address (prefectures in Japan). The traded category was classified, based on the transaction description, either for pet or food use. Details such as the collection location, colouration type, origin and number of individuals, were extracted from the transaction page descriptions and photographs. If specific information was unavailable, it was labelled as unverifiable. The colouration type was categorised into five groups: DB (dark brown), RD (red), SB (sky blue), OT (other colours) and Mix (a combination of several colour individuals, for example, DB and SB). In this study, colour classification was primarily based on the auction title and seller descriptions, as auction strategy relies on both sellers' and buyers' perceptions of colour. When no notes about colour were provided, carapace colouration from photographs attached in the auction page was used for categorisation into five colouration types in this study, given that *G. dehaani* species complex colour type is generally recognised by its carapace appearance. The basis of the case based on carapace colouration, was following DB: uniform dark brown carapace; RD: carapace with reddish parts at least; SB: carapace with sky-blue or white parts at least; and OT: carapace colouration that did not fall under the above categories. Consequently, this classification did not correspond to the colour definitions of previous studies that used not only carapace, but also pereiopods colourations (e.g. Chokki (1976, 1980)). In cases where neither colour notes nor photographs were available, the colour type was treated as unverifiable. Although less common colour patterns were observed (e.g. yellow and purple), their low frequency and irregular occurrence precluded detailed analysis; thus, they were grouped under the "other" (OT) type. To protect habitat conservation, specific data collection locality for the OT type was not disclosed in the results (e.g. Fig. 6; Suppl. materials 1, 2). The origin of the crabs was determined, based on the seller's description and the crabs were classified as wild-caught (WC), captive-bred (CB) or unverifiable (UN). The volume of WC individuals in online auctions served as an indicator of auction-related collection pressure in each prefecture, although it did not reflect the overall collection pressure. Sellers were categorised as amateurs (private sellers) or shops (vendors). The price-difference and the price per individual were calculated using the formulae of the opening-price minus closing-price and closing-price/number of individuals, respectively. All prices were reported in Japanese yen (JPY), with an average conversion rate of 114 JPY to 1.00 USD from January 2013 to December 2023.

Data analysis

Data analysis was performed using R version 4.3.1. with RStudio 2023.12.1 (RStudio Team 2020; R Core Team 2023). Statistical analysis included the Steel–Dwass test for multiple comparisons amongst the colouration types and log-transformed auction prices (opening-price, closing-price, price-difference and price-per-individual) following significant differences identified using the Kruskal–Wallis test.

A generalised additional model (GAM) assessed the non-linear annual fluctuations in two quantitative metrics: the number of individuals per deal and price-per-individual, excluding the RD type due to the limited transactions (n = 38). The model considered colouration type as a categorical predictor and allowed for separate smoothing functions over the years for each type. Response variables were log-transformed to approximate normality and to stabilise variance (i.e. log (number of individuals per deal) and log (price-per-individual + 1)). The Gaussian family was used with an identity link function and the smoothing parameter k = 9 was automatically selected by the gam() function in the mgcv package, based on the generalised cross-validation scores of 0.54 and 0.80 in models for the number of individuals per deal and the price-per-individual, respectively. Model significance and smoothing terms were evaluated using approximate *F*-tests, with a significance threshold set at $P < 0.05$. The GAM-predicted smooth curves with 95% confidence intervals and observed plots were visualised using the ggplot2 package.

Geographical distributions of the collection locations for each coloration type and the top sellers were visualised using QGIS version 3.34.1-Prizren (QGIS Development Team 2024). For manuscript preparation, ChatGPT 4.0 was used as an initial English proofreader before submitting the manuscript to a professional English proofreading service.

Results

The *G. dehaani* species complex had high demand as a pet in Japanese online auctions and wild individuals were sold in large quantities. During the 11-year assessment period, 46,319 individuals were traded in 3,431 transactions, generating total sales of 4,256,311 JPY (Suppl. material 2). The pet category dominated these transactions, comprising over 98% of the total deals, total individuals and total amount (JPY). Within the pet sector, WC individuals made up more than half of all deals, while CB individuals accounted for less than 1% of the totals. All CB individuals were SB colouration type, raised for over three years, with most CB transactions occurring in 2023. Eight distinct colour mix patterns were identified, mainly involving combination of the DB and RD colouration types (Suppl. material 3). All transaction of the *G. dehaani* species complex in the food category were of the Mix type.

Two transaction patterns emerged, based on body colouration traits: (1) high quantities with low price-per-individual for the DB and Mix types and (2) low quantities, but with high price-per-individual for the SB and OT types. The DB consistently surpassed other colour types in total deals and individuals and the number of individuals per deal (Fig. 1). While the DB type had medium opening – and closing-prices, it exhibited low price-difference and price-per-individual (Fig. 2; Steel-Dwass tests, DB-SB in DP: $W = -4.19$, $P = 0.02$; DB-SB in PPI: $W = 48.0$, $P < 0.001$), indicating a low unit price. The Mix type ranked second to the DB in both the numbers of deals and individuals (Fig. 1). In contrast, the SB exhibited higher transaction values across all measures, especially the price-per-individual (Fig. 2; Steel-Dwass tests; all combinations, except for SB-OT: $-7.89 < W < 7.87$, $P < 0.001$; SB-OT: $W = 1.19$, $P = 0.91$). Despite having an intermediate total deal, the SB's total individuals were lower due to fewer individuals per transaction (Fig. 1).

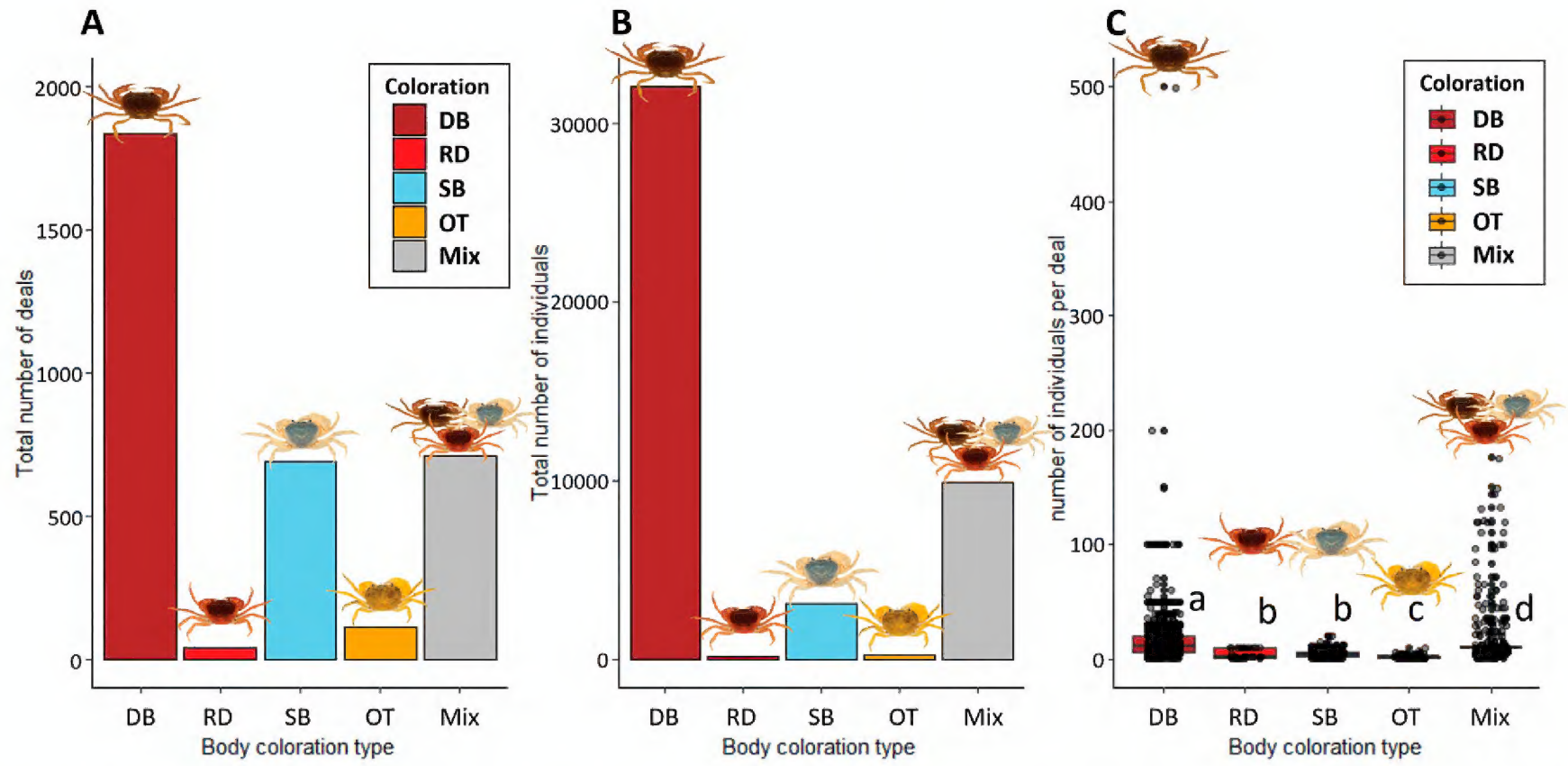

Figure 1. Differences in values of the *Geothelphusa dehaani* species complex. **A.** Total number of deals; **B.** Total individuals; **C.** Individuals per deal; **D.** Number of sellers. Bar colours represent the colouration types (dark brown: DB, red: RD, sky blue: SB, other: OT and Mix).

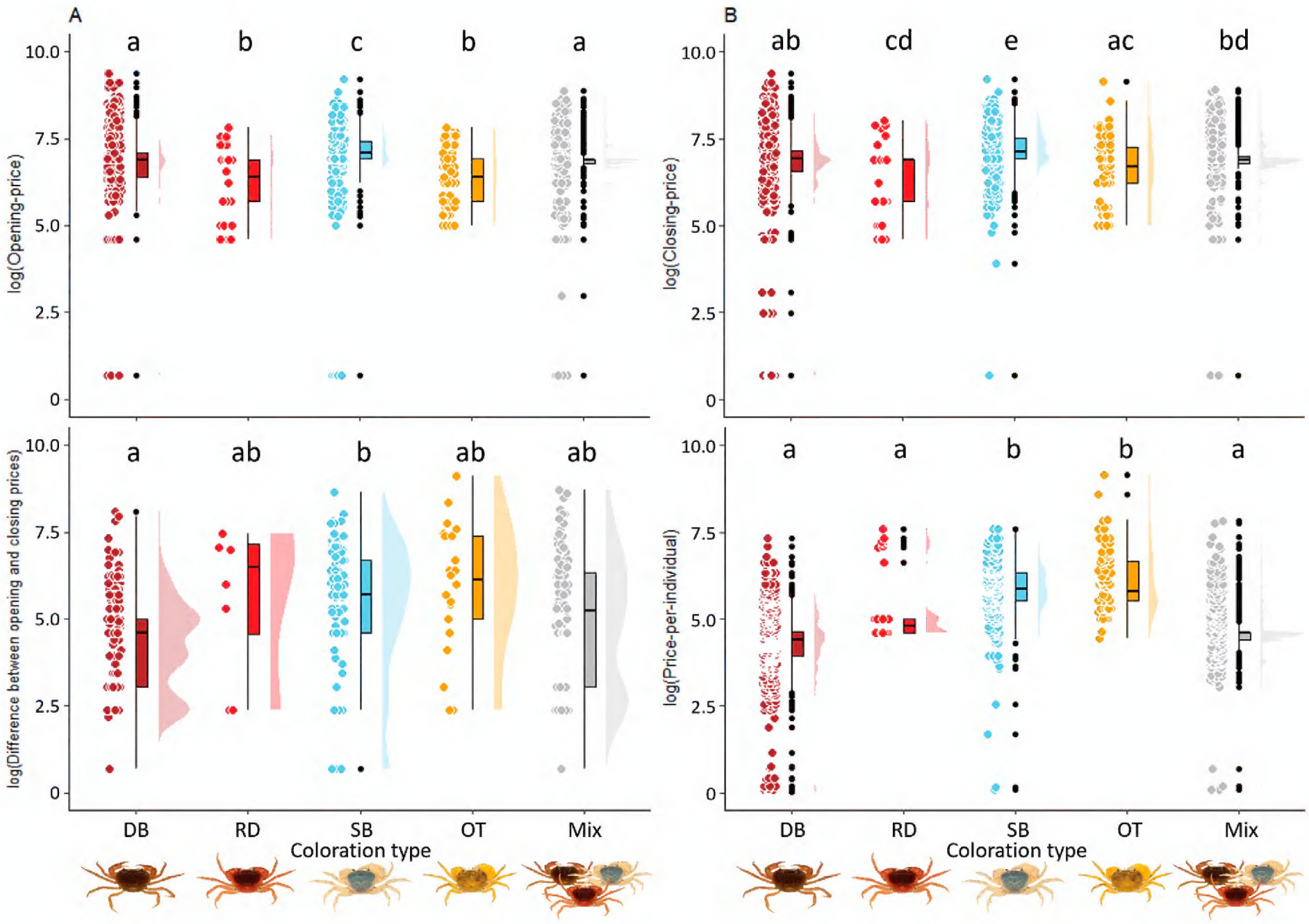

Figure 2. Comparison of the log-transformed prices of the *Geothelphusa dehaani* species complex in online auctions amongst the different colouration types. **A.** Opening-price; **B.** Closing-price; **C.** Difference between opening – and closing-prices; **D.** Price per individual. Abbreviations of the colouration type are shown and the box, central line, interval line from each box and circles indicate the 25th–75th quartiles, median, distribution from minimum to maximum and outlier values, respectively. Different letters indicate significant differences between groups, with $p < 0.05$.

While the OT showed higher price-per-individual (Fig. 2; Steel-Dwass tests; all combinations, except SB-OT: $-7.89 < W < 7.87$, $P < 0.001$), the opening – and closing-prices and the price-difference were not notably high and the OT had the lowest total individuals and number of individuals per deal amongst all colouration types (Fig. 1). Notably, the number of individuals per deal was greater for the DB and Mix types compared to the SB and OT types at equal closing-price (Fig. 3), supporting the distinct trends between colouration types.

Annual increases were observed in total deals, individuals and amounts, with marked surges in 2018 and 2020 (Fig. 4A–C). This growth was linked to an expansion in the number of sellers and transactions per seller, suggesting a synergistic effect (Fig. 4D). By colour, the DB showed a notable rise, trading 12,070 individuals for 594,340 JPY across 441 transactions in 2023, a significant leap from 2015 levels, which were similar to other colouration types. The SB also exhibited a recent increase in deals; though fewer individuals were traded, its value approached that of the DB by 2023.

GAMs revealed that temporal shifts in the number of individuals per deal and the price-per-individual varied, based on body colouration traits. Annual trends in the number of individuals per deal exhibited two distinct patterns: higher fluctuations in the DB and SB types and lower fluctuations in the OT and Mix types (Table 1; Fig. 5A). While the DB and SB types had similar values until 2015, their differences became increasingly pronounced over the years, with DB revealing an upward trend and SB a downward trend. The Mix type significantly surpassed the OT type. The price-per-individual also displayed annual colour-based trends, with DB exhibiting high fluctuation, but remaining consistently lower than the SB and OT types (Table 1; Fig. 5B). The Mix type showed a stable pattern, but similar values to the DB type.

The geographical distributions of WC individuals sold in online auctions varied by colouration types, with the DB and Mix showing widespread distribution, while the RD, SB and OT types were more localised (Fig. 6). Although the DA type reported by Chokki (1976) was widely distributed from Hokkaido to Kyushu (Kunishima and Takata et al. 2025), DB type transactions in this study were restricted to northern Kanto through Kyushu. Overall, no transactions were recorded in north-eastern Japan and high-volume deals were concentrated in western Japan, particularly in the Kinki Region (e.g. Kyoto, Wakayama and Hyogo prefectures). WC individuals from 29 prefectures south of Niigata and Tochigi comprised 2323 deals involving 27,297 individuals (Suppl. material 2). Regional differences in transaction numbers and individuals per deal reflected local geographical patterns in colouration type: the DB was present in 24 prefectures and the Mix in 13, while the RD, SB and OT types occurred in only 3, 8 and 7 prefectures, respectively. The DB type dominated in high-transaction prefectures (e.g. Kyoto and Wakayama), except in Tottori and Miyazaki prefectures where the Mix type prevailed (Fig. 6; Suppl. material 4). In contrast, the SB trades were confined to limited Pacific coastal areas (e.g. Chiba, Shizuoka, Kochi and Kagoshima) with few deals (Fig. 6). Sites with high DB deals (e.g. Kyoto) had more transactions than SB-dominant sites (e.g. Chiba), aligning with overall trends in the total deals for the DB and SB types. The OT type was sold sporadically, with 43.6% of its transactions lacking identifiable collection localities.

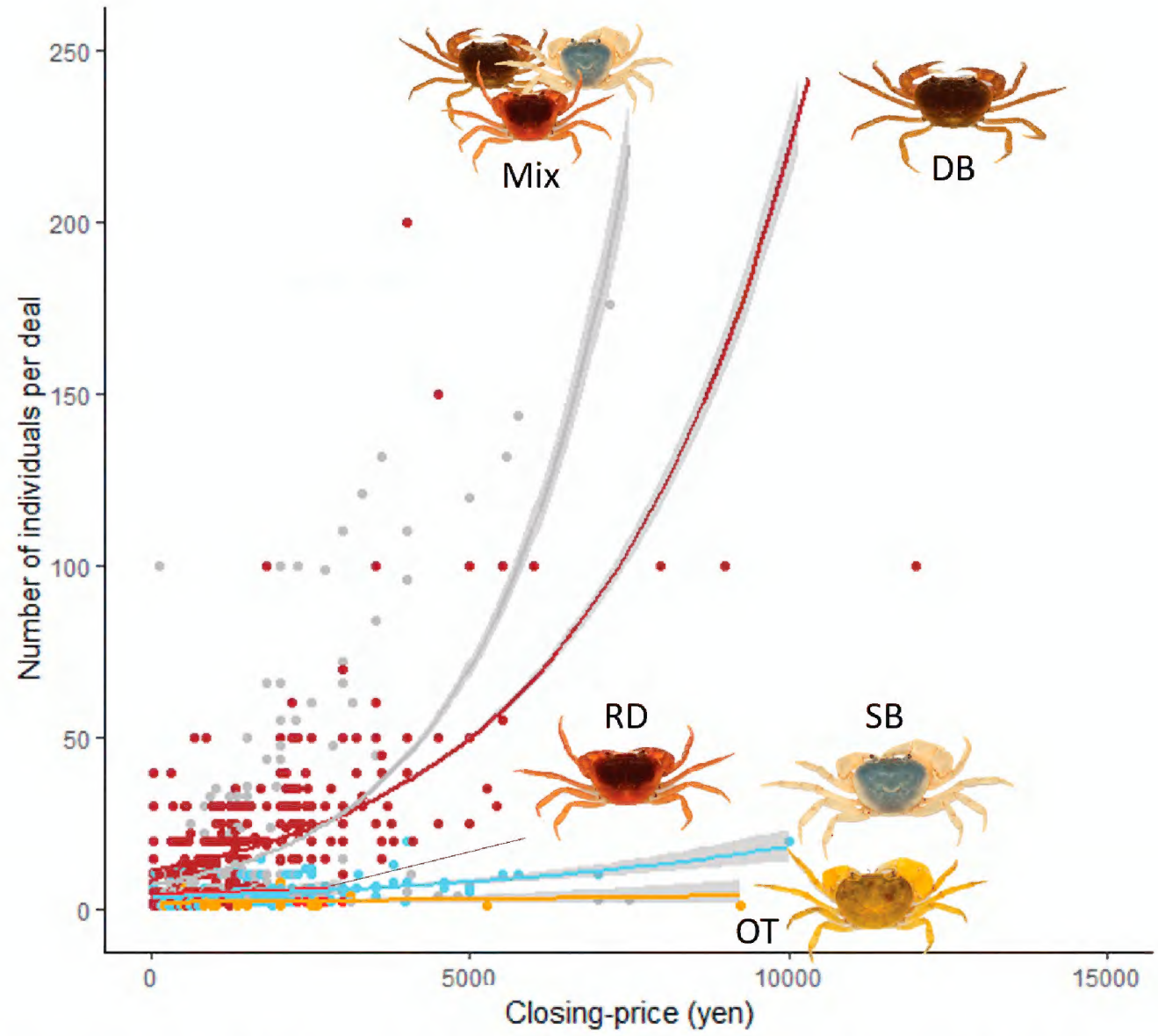

Figure 3. Relationship between the number of individuals per deal and closing-price for each colouration type of the *Geothelphusa dehaani* species complex. An extreme outlier (one dark brown (DB) transaction with over 500 individuals at 50000 yen) was excluded.

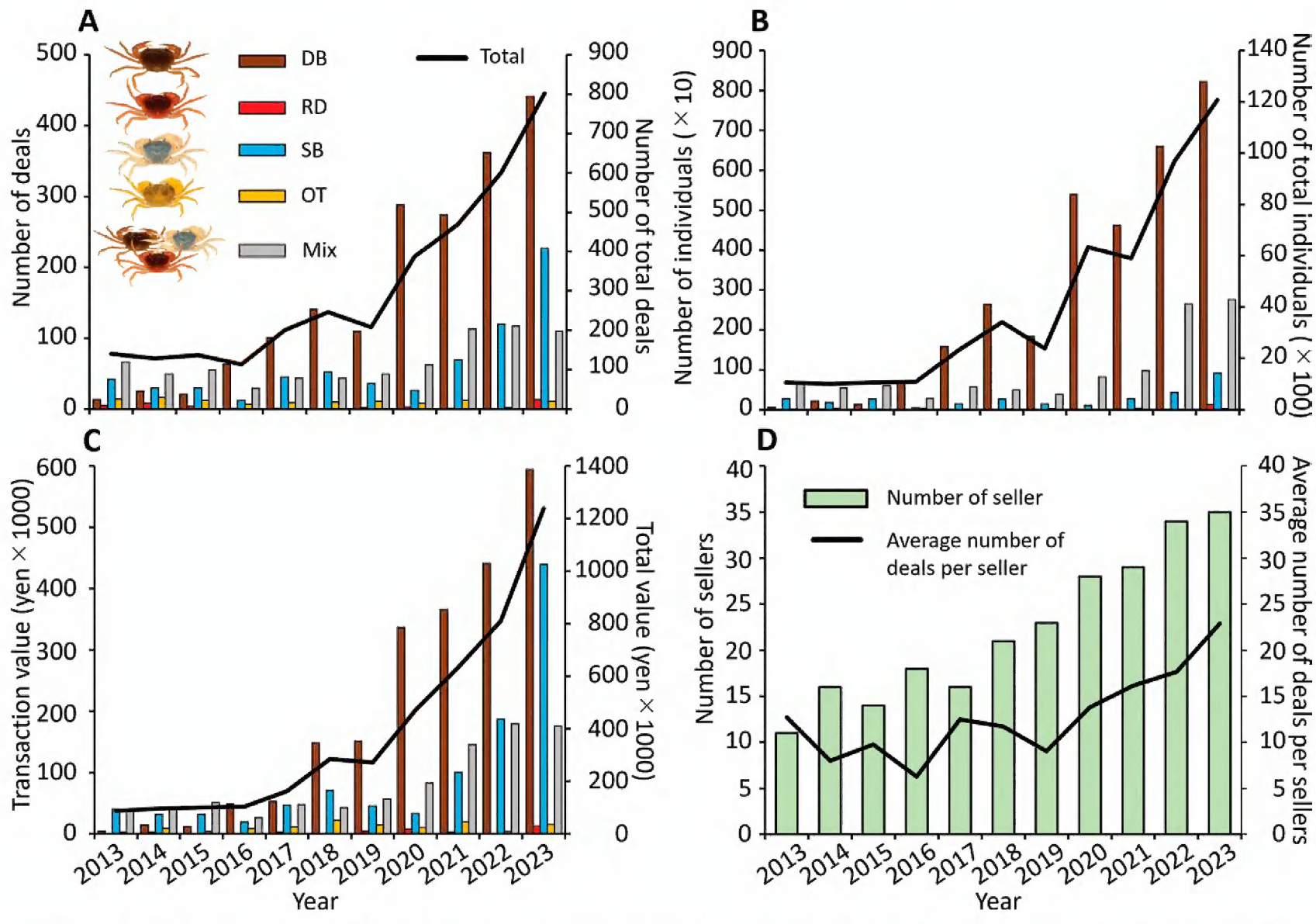

Figure 4. Annual trends in values of the *Geothelphusa dehaani* species complex. **A.** Number of deals; **B.** Number of individuals; **C.** Transaction value; **D.** Number of sellers. Bar colours denote the colouration types. The secondary axis in **A–C.** Indicates total values by year, while **D.** Shows the average number of deals per seller.

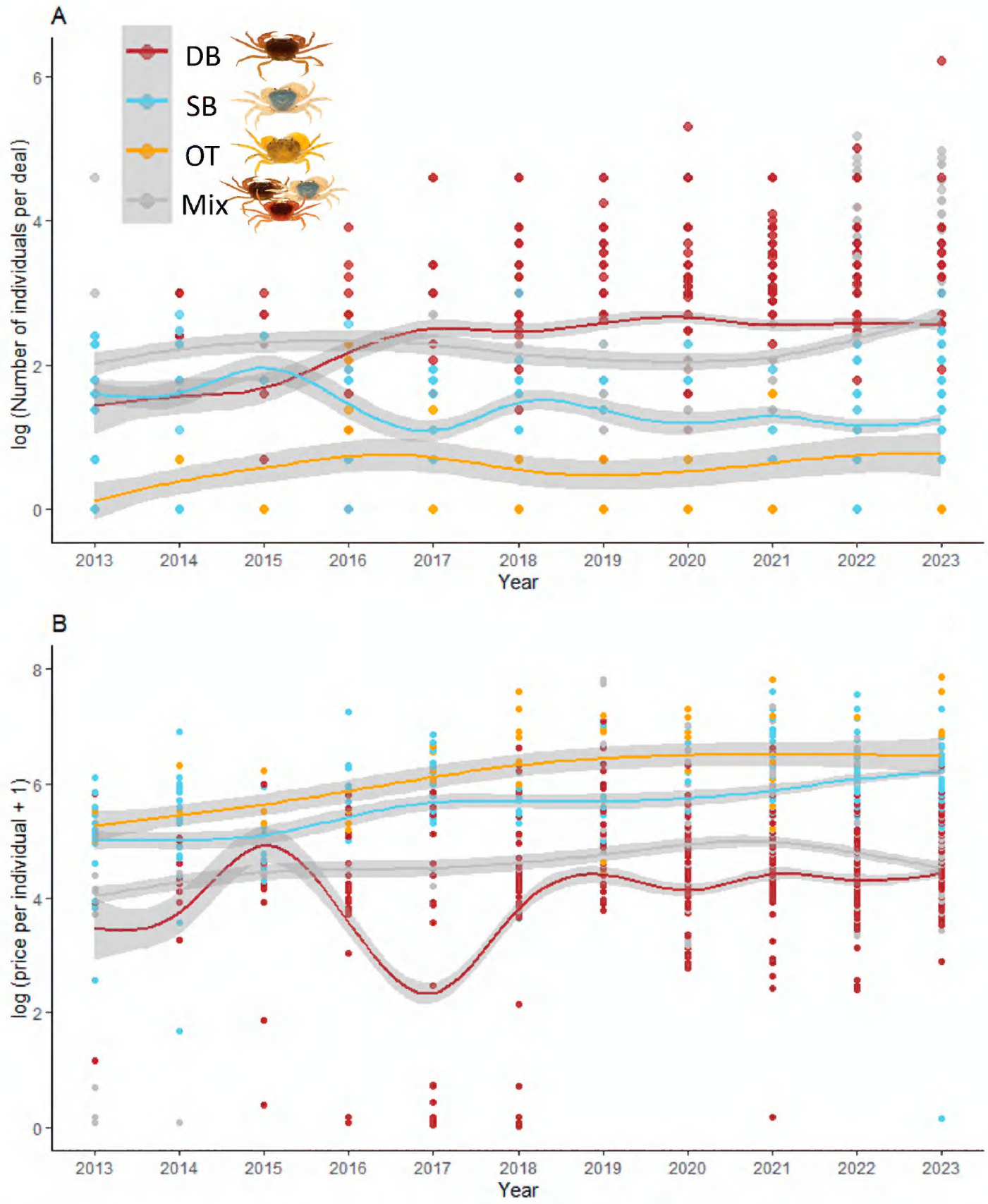

Figure 5. Temporal trends in traded numbers and price of the *Geothelphusa dehaani* species complex. **A.** Changes in the log-transformed number of individuals per deal from 2013 to 2023 were analysed using Generalised Additive Models (GAM). Each colour represents a different colouration type (dark brown: DB, sky blue: SB, other: OT and Mix). Shaded areas indicate the 95% confidence intervals; **B.** Log-transformed price per individual (+1) over the same period was also modelled with GAM. Points indicate individual observations and lines represent the fitted values for each colouration type.

Geographical tracking of sellers and the collection locations revealed that sellers tended to be unique to each area and operated with a monopolistic manner, particularly in high-transaction areas. Amongst the 139 sellers, 119 were non-professionals (85.6% of the total) and 96 completed only a single transaction. Of the 1,763 transactions with known collection sites, 93.7% (1,652 deals) matched the seller's location, suggesting most sellers collected the *G. dehaani* species complex locally (Suppl. material 5). Only six sellers sourced WC individuals from multiple locations, while 70 sellers operated from a single prefecture. In many areas, one seller dominated local transactions (Fig. 7; e.g. Tottori, Kyoto, Wakayama, Nagano and Chiba).

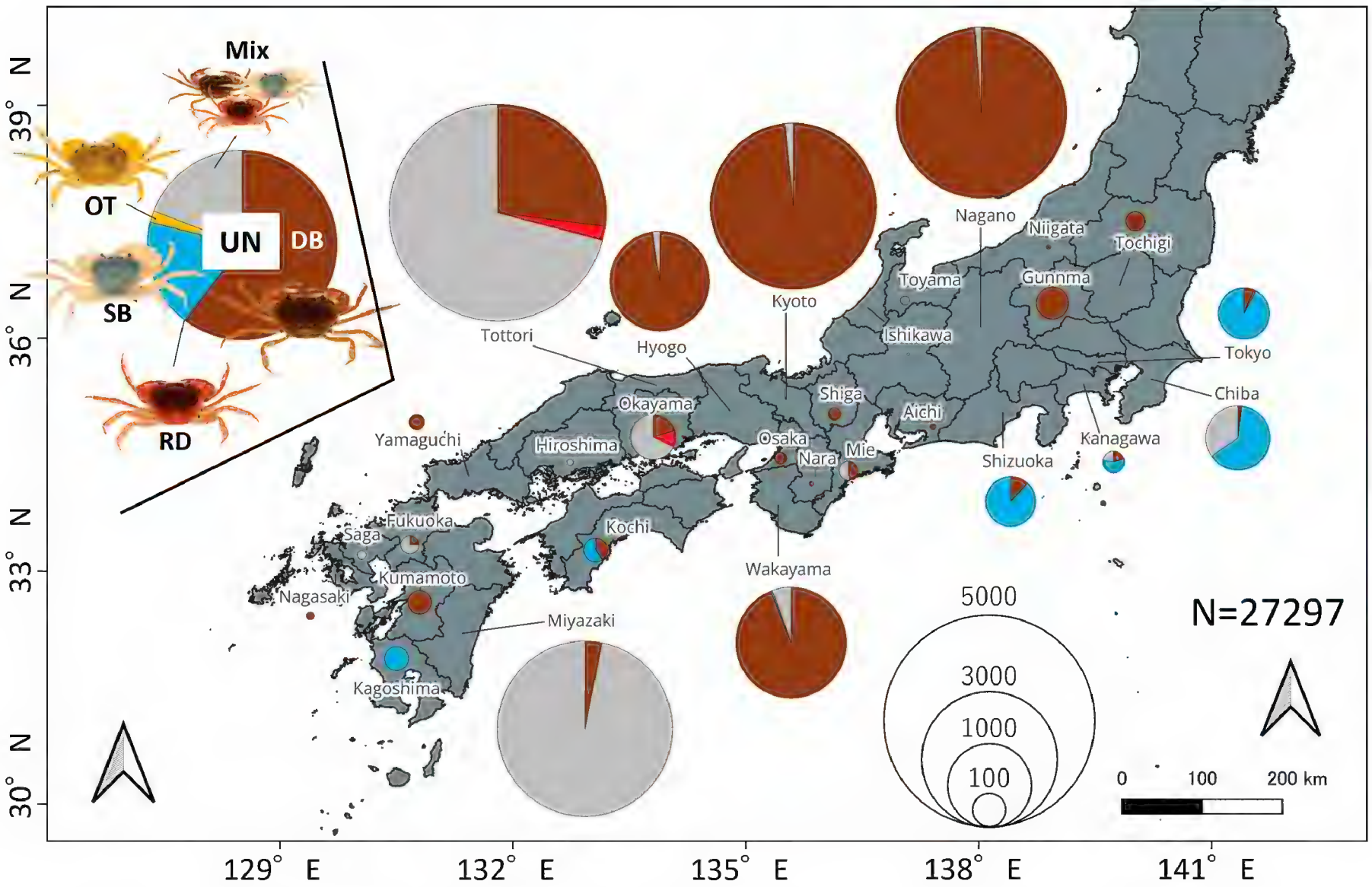

Figure 6. Map showing the geographical distributions and number of individuals by colouration type of the *Geothelphusa dehaani* species complex sold via Japanese online auctions (January 2013–December 2023). Circle sizes represent the number of deals.

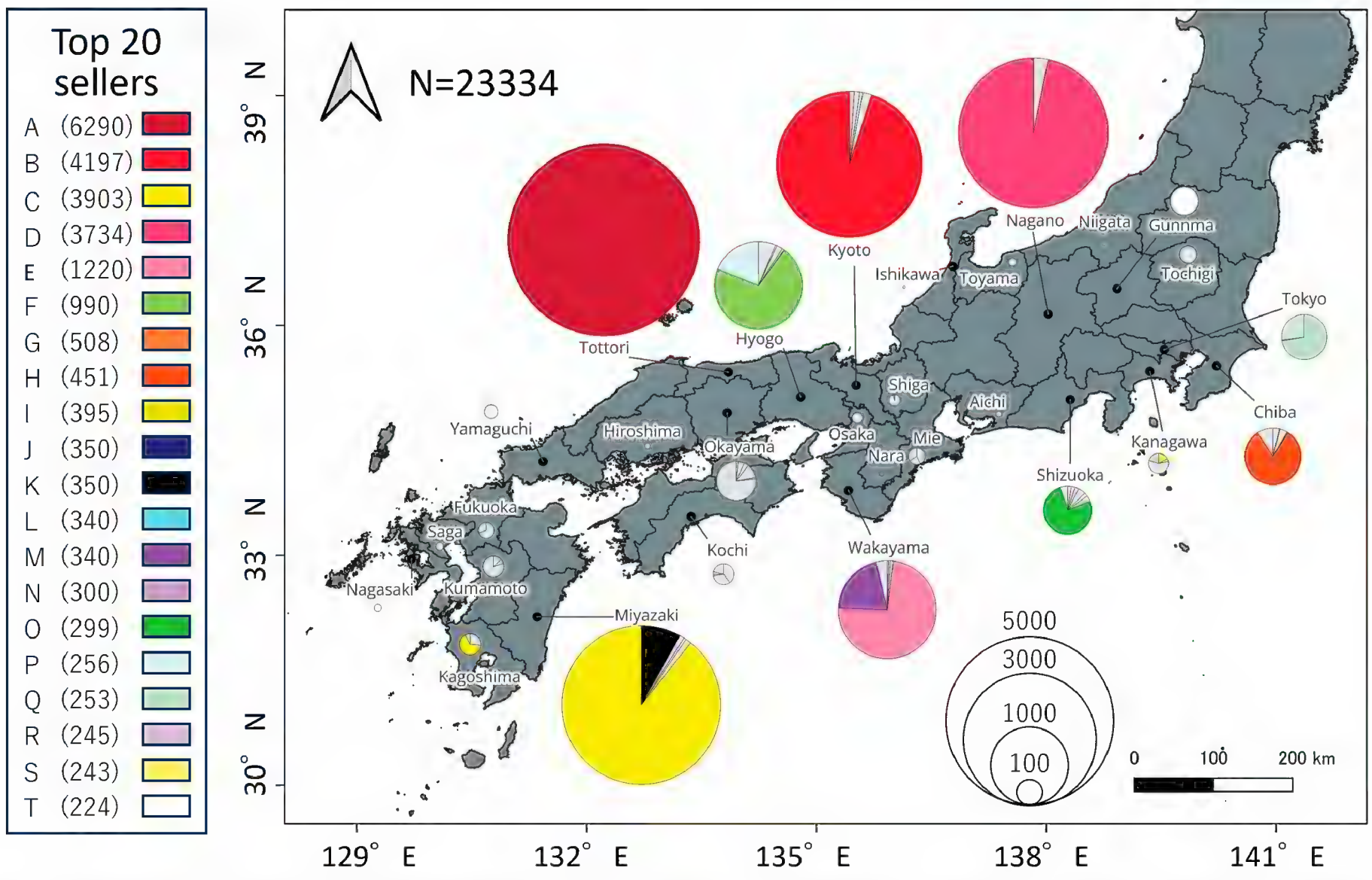

Figure 7. Map showing the geographical distribution of individuals sold by the top 20 sellers of the *Geothelphusa dehaani* species complex via Japanese online auctions (January 2013–December 2023). Circle sizes indicate the number of individuals sold. The identification number of sellers (A to T) and the number of deals is shown in parentheses.

Table 1. Generalised additive models. *F*-values, significance test *P*-values and estimated degrees of freedom (edf) are given for the colouration types against the temporal changes of two values: number of individuals per deal and price per individual. The adjusted R^2, deviance explained proportion (%) and generalised cross-validation scores (GCV) are also shown.

Parameters		Number of individuals per deal	Price per individual
Intercept	*t*	129.1	179.5
	Pr(>|*t*|)	< 0.0001	< 0.0001
	Estimate	2.439	4.13
s(year):colouration_DB	*F*	17.14	71.32
	P	< 0.0001	< 0.0001
	edf	7.932	8.800
s(year):colouration_RD	*F*	15.89	9.302
	P	< 0.0001	< 0.0001
	edf	2.823	3.130
s(year):colouration_SB	*F*	6.411	21.10
	P	< 0.0001	< 0.0001
	edf	8.582	5.390
s(year):colouration_OT	*F*	2.938	10.69
	P	0.001	< 0.0001
	edf	8.442	2.829
s(year):colouration_Mix	*F*	9.302	12.00
	P	< 0.0001	< 0.0001
	edf	8.490	4.744
n		3388	3388
R^2 adj.		0.411	0.470
Deviance explained (%)		41.8	47.5
GCV		0.540	0.795

Discussion

This study aimed to determine how body colouration traits and its geographical distribution of the *G. dehaani* species complex influence online auction sale strategies and collection pressure through online auctions on the wild individuals. Contrary to expectations, collection pressure via online auctions was higher for the common DB type than for the rarer SB and OT types (Fig. 6; Suppl. material 2). This resulted from the mechanism by two distinct strategies linked to the colour traits and its geographical distribution: a high-profit, low-sales (HPLS) strategy and a low-profit, high-sales (LPHS) strategy.

The first mechanism involves reducing the number of individuals collected through the HPLS strategy, which is a high-value-addition strategy. This strategy entails selling a small number of individuals at a high price per unit and applies to transactions that involve locally distributed, rare types, such as the SB and OT types. In the case of the SB and OT types of the *G. dehaani* species complex, the total number of individuals, collected from the wild populations, was lower than that from the DB populations, thus indicating a reduced collection pressure via online auction (Suppl. material 2). Conversely, the number of deals has remained stable over the years (Fig. 4) and opening value of SB and OT types was significantly higher than those of DB and Mix types (Fig. 2), which

suggests that sellers from the SB distribution areas have adopted a strategy of maintaining high unit prices by limiting the supply relative to the demand, thus earning high profits from a small number of individuals. HPLS strategy applied to both OT and SB types; however, the lower supply of the OT type may appear due to small number of individuals in nature, unlike the SB type. This HPLS strategy is commonly employed in the market and can be applied to the sale of living organisms. Furthermore, the HPLS strategy may stimulate cultivation because of its high unit price. The number of CB individuals in the SB type increased in 2023 (Suppl. material 2), likely as a by-product of the high-unit-price sales strategy. Wildlife farming has been advocated as a means to conserve overharvested species, as it may prevent illegal hunting, depending on market conditions (Bulte and Damania 2005; Phelps et al. 2014). Given these considerations, the HPLS strategy may maintain the relatively lower collection pressure via online auctions on the SB and OT type individuals, at the present stage.

The second mechanism involves increased collection pressure via online auction, through a LPHS strategy. This applies to the DB type, which has a wide distribution and high generality, as well as the Mix type, which contains multiple colour types. As the DB type is more common with wide distribution than the SB and OT types and has a lower unit price (Fig. 3), it is likely that sellers within these distribution regions have selected this strategy of trying to generate a profit by increasing the number of individuals sold per deal. The LPHS strategy increases collection pressure via online auction because of the large number of individuals that are sold. Indeed, Takaku and Morosawa (2021), who classified the marketing strategies for endangered Japanese freshwater fish, similarly found a type of LPHS strategy and indicated that there is concern regarding the increased collection pressure on this type of fish species because many WC individuals were sold.

The present study suggests that wildlife biological traits such as body colouration can drive the human behaviour on the market (i.e. sale strategies). Furthermore, the findings highlight the potential for auction strategies to create heterogeneity in collection pressure by being influenced by the biological traits and distribution patterns of target organisms. While many studies have investigated the effects of auction sales on wildlife, few have explicitly linked these dynamics to the spatial distribution of biological traits and collection pressure heterogeneity (Lyons and Natusch 2013; Militz et al. 2018). Understanding these connections is vital for mitigating the impact of auction sales on biodiversity, as the spatial distribution of organisms for sale is a key indicator for collectors when establishing their collection strategies (Militz et al. 2018). For instance, if rare species or colour morphotypes are distributed non-randomly, collectors may adopt targeted collection strategies, which may potentially lead to the decline of specific populations (anthropogenic Alee effects: AAEs; Courchamp et al. (2006); Holden and McDonald-Madden (2018)). Conversely, a random distribution may encourage a focus on more common species or morphotypes, thereby increasing the likelihood of opportunistic exploitation (Branch et al. 2013). In the case of the *G. dehaani* species complex, colouration types exhibited a non-random distribution pattern that varied regionally, with rare and common types generally not co-existing (Suppl. material 2; Fig. 6). Consequently, different marketing strategies result in constant collection pressure via online auctions on specific colour types. This phenomenon is not limited to rare species, but also extends to mediate-demand, mass-consumed

organisms, which highlights the concerns about non-rare species by revealing their inter – and intra-specific rarity. Given the prevalence of geographically isolated colour polymorphisms and variations, including mammals, birds, reptiles, amphibians, fish and insects (Galeotti et al. 2003; Hoekstra et al. 2004; Mochida 2009; Lyons and Natusch 2013; Militz et al. 2018; Araki and Sota 2021), it is plausible that collection pressure heterogeneity resulting from varied auction sales strategies may be widespread across diverse taxa. Therefore, this study highlights the need for the recognition and monitoring of colour polymorphic organisms traded via online auctions.

This study discusses how two strategies influence the local collection pressures via online auctions; however, these dynamics may shift dramatically with the emergence of a mass seller. As a countermeasure, the author proposes establishing an annual limit on the number of living animals auctioned per species for the online auction platform. Fig. 7 and Suppl. material 6 indicate that local sellers were often monopolised by a few entities, which suggests that the transaction volumes can easily change, based on sellers' intentions and types of behaviour. With the rapid development of the internet, information is widely accessible and "good practice" in online auctions can be easily referenced. Indeed, even though the DB type is overwhelmingly predominant, if it turns out that sellers in areas with no transactions (north-eastern Japan) or very low transaction volumes (such as Nara and Yamaguchi) can obtain high economic incentives through mass selling (i.e. employing the LPHS strategy), those areas may quickly ascend in the ranking of traded individuals. Banning the wildlife trade under national or regional laws is a common approach to reduce the collection pressures. However, prohibiting sales for certain popular species may inadvertently lead to an increased trade of alternative species (Kubo et al. 2025). Therefore, more nuanced restrictive measures may be more effective.

In addition, future taxonomic revision for this species complex may also alter the dynamics of colour-based sales strategies. Recent phylogenetic studies classified the *G. dehaani* sensu lato into five populations which have distinct geographical boundaries (Kunishima and Takata et al. 2025; HO, SHI, nK, cK and sKK populations) and suggest the presence of the cryptic species (Takenaka et al. 2023). If these populations are described as a new species, the seller might capitalise on their novelty and rarity to command higher prices (Altherr and Lameter 2020). Indeed, some recent transactions on the *G. dehaani* species complex have advertised rarity and unique population affinities; for instance, the SB type from Amakusa Islands, Kumamoto Prefecture (likely *G. amakusa*), was sold in online auction with explicit notes on its rarity (Kunishima, pers. obs.). Moreover, heterogeneity in collection pressure via online auction should be also considered in order to establish conservation strategies when their taxonomic status is changed. Kunishima and Takata et al. (2025) reveal that each colour type of the *G. dehaani* species complex, as defined by Chokki (1976), comprises multiple populations: the DA type includes four populations, while the BL type includes two populations, respectively. Currently, the HPLS strategy appears to maintain low collection pressure via online auctions on the SB type of the *G. dehaani* species complex (Figs 3, 6). However, the concentration of transactions in southern Kanto and Shizuoka, where the sKK population in Kunishima and Takata et al. (2025) is distributed, suggests potential overexploitation risks if this population gains additional value as a new species. Conversely,

high DB collections in western Japan are linked to the HO population, which is widely distributed across Hokkaido, Honshu and Shikoku Islands (Kunishima and Takata et al. 2025). Given that *G. dehaani* sensu lato requires four years to mature (Araki and Matsuura 1995) and that species with longer to maturation periods are generally more vulnerable to collection pressure, continued mass collection through LPHS strategies may negatively impact the DB-related HO populations of Kunishima and Takata et al. (2025). Consequently, for species or species complex which indicated the existence of cryptic species or deeply divergent populations, it is essential to assess both the demand for their biological traits and its spatial distribution pattern in wildlife trades, while proactively considering measures to mitigate potential subsequent impacts on the wildlife trades due to changes in the taxonomic status. Such vigilance is crucial to anticipate and mitigate shifts in the market dynamics that could exacerbate collection pressures on vulnerable species or populations.

In this study, while transaction data indicate varying collection pressure via online auctions on the *G. dehaani* species complex by body colouration traits, the actual impact on wild populations was not tested because of a lack of wild population parameters, such as abundance and density. As suggested by Challender et al. (2022), research using only trade data must avoid the mischaracterisation of the threat that trade poses to certain species or groups and the misinterpretation of wildlife trade data. Accurately evaluating the impact of wildlife sales via online auctions requires a multifaceted approach, combining auction data with field data for the target species. For the *G. dehaani* species complex, limited field data on population density, distribution and genetic structure emphasise the need for further research (Nakajima and Masuda 1985; Aotsuka et al. 1995; Takenaka et al. 2023; Kunishima and Takata et al. 2025). Therefore, the next step of this research should be to establish their population size and dynamics to assess the impact of colour-based collection pressure via online auctions. Such an integrated approach is vital for mitigating exploitation risks from wildlife trade and ensuring sustainable interactions between commerce and conservation.

In addition to enhancing field information on the targeted species' status, a deeper understanding of demand mechanisms is also required. This study suggests the possibility that distinct marketing strategies resulting from colour variation may reflect different customer needs. Specifically, the SB and OT types were in high demand as pets, while the DB and Mix types fulfilled both food and pet food demands. The observation that several items in the pet category were advertised as food items and that all *G. dehaani* sensu lato in the food category were of the Mix type (composed of only DB and RD types) may support this hypothesis. In Japan, *G. dehaani* sensu lato is eaten in some mountainous regions, but the SB type is not consumed in the areas where it lives (Chokki 1993). If an edible demand exists only for specific colour types, it indicates that different colours within a species could create varying demands, which suggests a more complex relationship between body colouration traits and consumer preferences. However, the limited number of food categories identified in this study due to the sole use of online auction data lacks sufficient objective evidence (Suppl. material 2). Additional surveys for the *G. dehaani* species complex sales as food items in both in-store and online and further analysis may clarify this point.

Conclusions

This study analysed transaction data from online auctions, focusing on how body colour traits affect sales strategies for the *G. dehaani* species complex and changes the collection pressure via online auctions in relation to these geographical distributions. The results of this study demonstrate that the interplay between colour variation and the geographical distribution of the *G. dehaani* species complex significantly shapes sale strategies and the resulting heterogeneity in online auction related collection pressure on wildlife populations. The results reveal that, for rarer types such as SB and OT, sellers tend to adopt a high-profit, low-sales (HPLS) strategy that limits the number of individuals sold while maintaining high unit prices. This approach results in relatively lower collection pressures via online auctions, despite having the narrow distribution range in certain types, particularly the SB type. In contrast, for more common types like DB and Mix, a low-profit, high-sales (LPHS) strategy is employed, characterised by the sale of a larger number of individuals at lower prices per unit, which leads to increased collection pressure via online auctions, especially for the widely distributed DB type. These findings underscore how marketing strategies driven by inherent biological traits and its geographical distribution can create heterogeneous collection pressures that may put vulnerable populations at risk. Furthermore, the study points out the need for integrating auction data with field-based research on population density and genetic structure to accurately assess the impacts of wildlife trades, including online auction. Such an integrated approach is essential for devising targeted monitoring programmes and effective conservation strategies and suggests that implementing nuanced regulatory measures, such as annual limits on the number of living animals auctioned per species, could help mitigate the risks associated with these varied collection pressures under wildlife trades.

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Additional information

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The author declares no competing interests.

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For manuscript preparation, ChatGPT 4.0 was used as an initial English proofreader before submitting the manuscript to a professional English proofreading service.

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Author contributions

T. Kunishima: conceptualisation, investigation, data curation, methodology, formal analysis, visualisation, writing – original draft and writing – review and editing.

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Data availability

All data analysed during the present study are included in this paper. If raw data files in other formats are required, they can be obtained from the responsible author upon reasonable request.

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Supplementary material 1

Photographic examples of each colouration type of the *Geothelphusa dehaani* species complex

Authors: Taiga Kunishima

Data type: tif

Explanation note: Note: other colour (OT) type includes various patterns, not just yellow individuals (e.g. purple, pink and spotted patterns). Photographs provided by Shigetomi Matsuno (Wakayama Prefectural Museum of Natural History).

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Link: https://doi.org/10.3897/natureconservation.59.142085.suppl1

Supplementary material 2

Transaction information for the *Geothelphusa dehaani* species complex sold via Japanese online auctions (January 2013–December 2023)

Authors: Taiga Kunishima

Data type: docx

Explanation note: including the category (pet or food), origin (wild caught: WC, captive-bred: CB or unverifiable: UN), Prefecture of collection, number of deals, total individuals and total sales volume for each colouration type. To protect the habitats, numbers of deals, total individuals and total sales for OT type and each Prefecture were not disclosed in this table.

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Link: https://doi.org/10.3897/natureconservation.59.142085.suppl2

Supplementary material 3

Breakdown of the Mix type of the *Geothelphusa dehaani* species complex sold via Japanese online auctions (January 2013–December 2023)

Authors: Taiga Kunishima

Data type: docx

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Supplementary material 4

Map showing the geographical distribution of the frequency and degree of deals associated with each colouration type of the *Geothelphusa dehaani* species complex via Japanese online auctions (January 2013–December 2023)

Authors: Taiga Kunishima

Data type: tif

Explanation note: Circle sizes represent the number of deals. To protect the habitats, numbers of deals, total individuals and total sales for OT type and each Prefecture were not disclosed in this map.

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Link: https://doi.org/10.3897/natureconservation.59.142085.suppl4

Supplementary material 5

Number of deals showing the relationship between collection sites and shipping addresses of the *Geothelphusa dehaani* species complex sold via Japanese online auctions (January 2013–December 2023)

Authors: Taiga Kunishima

Data type: docx

Explanation note: Bold and underlined figures indicate transactions where the collection sites and shipping addresses coincide. Amateurs are indicated with figures, while those in parentheses represent aquarium shops as sellers. Prefecture abbreviations: MG, Miyagi; AK, Akita; YG, Yamagata; TC, Tochigi; GU, Gunma; ST, Saitama; CB, Chiba; TY, Tokyo; KN, Kanagawa; NI, Niigata; TM, Toyama; IS, Ishikawa; YN, Yamanashi; GI, Gifu; NA, Nagano; SZ, Shizuoka; AI, Aichi; ME, Mie; SI, Shiga; KY, Kyoto; OS, Osaka; HG, Hyogo; NR, Nara; WA, Wakayama; TT, Tottori; OY, Okayama; YA, Yamaguchi; TK, Tokushima; EH, Ehime; KO, Kochi; FO, Fukuoka; MZ, Miyazaki and KG, Kagoshima.

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Link: https://doi.org/10.3897/natureconservation.59.142085.suppl5

Supplementary material 6

Map illustrating the geographical distribution of the frequency and degree of deals by the top 21 sellers of live *Geothelphusa dehaani* species complex via Japanese online auctions (January 2013–December 2023)

Authors: Taiga Kunishima

Data type: tif

Explanation note: Circle sizes indicate the number of deals. The identification number of the top 21 sellers (A to U) and the number of deals in parentheses.

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